

Effect of forest canopy on GPS-based movement data

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Abstract The advancing role of Global Positioning System (GPS) technology in ecology has made studies of animal movement possible for larger and more vagile species. A simple field test revealed that lengths of GPS-based movement data were strongly biased ($P < 0.001$) by effects of forest canopy. Global Positioning System error added an average of 27.5% additional length to tracks recorded under high canopy, while adding only 8.5% to open-canopy tracks, thus biasing comparisons of track length or tortuosity among habitat types. Other studies may incur different levels of bias depending on GPS sampling rates. Ninety-nine percent of track errors under high canopy were ≤ 7.98 m of the true path; this value can be used to set the scale-threshold at which movements are attributed to error and not biologically interpreted. This bias should be considered before interpreting GPS-based animal movement data.

Key words animal movement, forest canopy closure, Global Positioning System, GPS error, GPS-tracking, snow-tracking, tortuosity

The study of animal movement can be motivated by a variety of research questions. Movement data have been collected to study foraging patterns (McIntyre and Wiens 1999, Pochron 2001, Nolet and Mooij 2002, Fauchald and Tveraa 2003), identify behavioral differences across groups (With 1994a,b; Bascompte and Vilà 1997; Bergman et al. 2000), and reveal effects of differing habitat regimes on populations (With 1994b, Ferguson et al. 1998, Doerr and Doerr 2004, McDonald and St. Clair 2004). Many of the field and analytic techniques developed in studies of movement have focused on invertebrate (Kareiva and Shigesada 1983, Turchin et al. 1991) or small vertebrate (Leman and Freeman 1985, Edwards et al. 2001) populations at local scales. However, the advancing role of Global Positioning System (GPS) technology in ecology has made such studies possible for larger and more vagile species. This includes the direct deployment of GPS units on study animals (Bergman et al. 2000, Biro et al. 2002, Weimerskirch et al. 2002) and the use of handheld GPS units to record movements, as in snow-tracking (Ciucci et al. 2003).

The rise of GPS tracking in collecting animal movement data has brought with it much need for evaluation of accuracy and bias. Many authors have documented discrepancies in GPS fix rates and location accuracy of wildlife GPS collars caused by terrain and forest canopy (Moen et al. 1996, D'Eon et al. 2002, Di Orio et al. 2003, Frair et al. 2004), though results are not entirely consistent (Rempel et al. 1995, Dussault et al. 1999, Bowman et al. 2000). These evaluations of GPS are based on individual points. As the link between GPS and analysis of animal movement continues, testing must progress to evaluate how these factors affect a more complex line, or track, of GPS data.

We encountered this issue when overlaying a data set of lynx (*Lynx canadensis*) tracks, collected through snow-tracking, on habitat layers in a Geographic Information System (GIS). Many tracks showed differences in "tortuosity" or "sinuosity" (Turchin 1998, McDonald and St. Clair 2004) between open-canopy habitats and closed-canopy forest stands. Movement through openings appeared linear and direct, while movement through closed-canopy forest was more tortuous

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and wandering. Differential tortuosity in animal movements across habitat patches may be indicative of prey density or habitat quality (Zach and Falls 1976, Edwards et al. 2001, Nolet and Mooij 2002, Fortin 2003) or of foraging patterns like the area-restricted (or area-concentrated) search (Walsh 1996, Fortin 2003). However, the patterns in our data also may have been the misleading effect of disparate GPS accuracy across habitat types. It is important to address this issue before interpreting GPS-based wildlife tracking data.

We conducted a simple field test to quantify the effect of forest canopy closure on our GPS tracking data by collecting a test data set in the field. These data elucidate the effect of canopy on our GPS tracking, as well as the scale at which this effect is important.

Study area

We collected these data in the Clearwater River drainage of the Lolo National Forest, near Seeley Lake, Montana (N 47° 11', W 113° 29'), roughly 50 km northeast of Missoula, Montana. Elevations on the study area ranged from 1,200–1,900 m, and the average slope of data collection sites was 7.5 degrees. Low-elevation forests were dominated by Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), and ponderosa pine (*Pinus ponderosa*), usually as mixed stands. Upper-elevation forests were mostly subalpine fir (*Abies lasiocarpa*), whitebark pine (*Pinus albicaulis*), and Engelmann spruce (*Picea engelmannii*) with lesser components of lodgepole pine, Douglas-fir, and western larch. Subalpine forests were multi-storied and multi-aged, often with a dense shrub understory (United States Forest Service 1997).

Methods

Data collection

During December 2003 and January 2004, we collected a data set of test tracks by using compass bearings to walk straight lines across the landscape. For each line we classified overhead forest canopy closure into 1 of 3 simple categories: open (0–10%), low (11–39%), and high (>40%). We selected areas where classification into these categories was unequivocal and boundaries between categories were clear, such as where frozen lakes or logged units abutted denser forest stands. We attempted to

hold constant travel speeds between categories and collected data during a range of dates and times between 16 December 2003, and 28 January 2004, and between 0830 and 1630 hrs. We collected all data with 4 Trimble GeoExplorer® 3 data logging GPS units (Trimble Navigation Ltd., Sunnyvale, Calif.) and Trimble external antennae mounted at roughly 1.8 m above ground. The units were configured with a 2-second log interval between points, and we differentially corrected data using Trimble GPS Pathfinder® Office software. Base station data came from multiple TRS base stations within 260 km of our study area using 1-second and 5-second logging rates.

Effect of canopy

We collected 95 straight-line tracks ($n_{\text{open}}=40$, $n_{\text{low}}=19$, $n_{\text{high}}=36$) totaling 19.9 km of GPS length. For each GPS recorded track, we required a paired “true” track to represent the actual distance traveled without GPS error. We initially quantified this distance with a straight line connecting the first and last points of each GPS track. Because we walked only straight lines in collecting GPS tracks, we knew any fine-scale deviation from straight represented error. However, the GPS tracks also showed very gradual bends away from the straight lines, due to difficulties in maintaining a consistent compass bearing over hundreds of meters. These gradual bends were a potentially confounding source of error, and we objectively controlled for this by creating “true” tracks using the Bezier smoothing algorithm in the ET GeoWizards® extension (www.ian-ko.com) for ArcGIS® Desktop 8.3 (Environmental Systems Research Institute, Inc., Redlands, Calif.). We found the Bezier algorithm removed all fine-scale GPS scatter and fitted a smoothed line over the actual path (whether straight or gradually bending); thus, we assume this accurately represented the true track. We then used the lengths of the original GPS track and the smoothed, true track to calculate an index ($\hat{\epsilon}$) of GPS error:

$$\hat{\epsilon} = 1 - (\text{true length}/\text{GPS length}).$$

Each value of $\hat{\epsilon}$ represents the proportion of a track's original GPS length that is attributable to error.

We used one-way univariate analysis of variance (ANOVA) and the type III sums of squares *F*-test to assess differences in error among categories of

canopy closure. Given a significant ANOVA result, we used the Tukey test (Tukey 1953) as a *a posteriori*, multiple-comparison test of differences between canopy categories (Zar 1999).

Scale of error

We separated each GPS track into the network of individual GPS points, or vertices, that were sequentially collected in making it. We then used the Nearest Features v. 3.6d (www.jennessent.com/downloads/NearFeat.zip) extension in ArcView GIS 3.2a to compute the perpendicular distance of each vertex from our smoothed, true track. We expected correlation among error distances within each track and, thus, computed distribution-free tolerance intervals, containing 99% of the population of error distances with 95% confidence (Hahn and Meeker 1991). These tolerance intervals represented the range of movement attributable to error within each canopy category, or more importantly, the scale-threshold at which movements could be biologically interpreted.

Confounding sources of error

We acknowledged several additional sources of GPS error that had the potential to confound our analysis of canopy closure and error. The Trimble GeoExplorer 3 units have standard precision of 1–5 m with differential correction (Trimble Navigation, Ltd. 1999) and the smoothing procedures used to generate our “true” tracks have an unknown error. However, we can assert that these sources of error were objective and unbiased across habitat types.

Differences in user speed, topography, and hourly satellite availability across habitat types could also confound this analysis. For each track we quantified user speed in meters walked per second, topography as the slope of each track centroid, and satellite availability as the number of available satellites and the available Position Dilution of Precision (PDOP), a metric of satellite geometry, based on daily satellite almanacs in the Quick Plan operator of Trimble GPS Pathfinder Office software. We then used one-way ANOVA and the type III sums of squares *F*-test to look for confounding differences across canopy-closure categories.

Satellite almanacs provided a measure of the available satellite configuration for our study area at a given time. However a GPS unit needs a clear view of the sky to access the full array of availability predicted by the almanac. Given insignificant differences in the predicted availability for tracks

recorded in different canopy types, we performed a final test using the maximum PDOP values recorded for each GPS track. We used one-way ANOVA to test if this metric of precision was affected by canopy closure, as a concluding test of the effects of canopy closure on GPS error.

Results

Effect of canopy

Mean error index values (SE) for each canopy category were: $\bar{e}_{\text{open}} = 0.085$ (0.016), $\bar{e}_{\text{low}} = 0.154$ (0.033), and $\bar{e}_{\text{high}} = 0.275$ (0.028). Thus, GPS error accounted for an overestimation of track length from 9–28% depending on canopy closure. Boxplots revealed a positive trend between increasing canopy closure and GPS error (Figure 1), and ANOVA sums of squares *F*-test results suggested canopy was a significant ($F_{2,92} = 17.78$, $P \leq 0.001$) variable in predicting GPS error. Tukey multiple comparison tests of differences between canopy categories revealed strong differences between open and high ($\bar{y}_{\text{high}} - \bar{y}_{\text{open}} = 0.190$, $P < 0.001$) and low and high ($\bar{y}_{\text{high}} - \bar{y}_{\text{low}} = 0.121$, $P = 0.008$), and no difference between open and low ($\bar{y}_{\text{low}} - \bar{y}_{\text{open}} = 0.070$, $P = 0.178$).

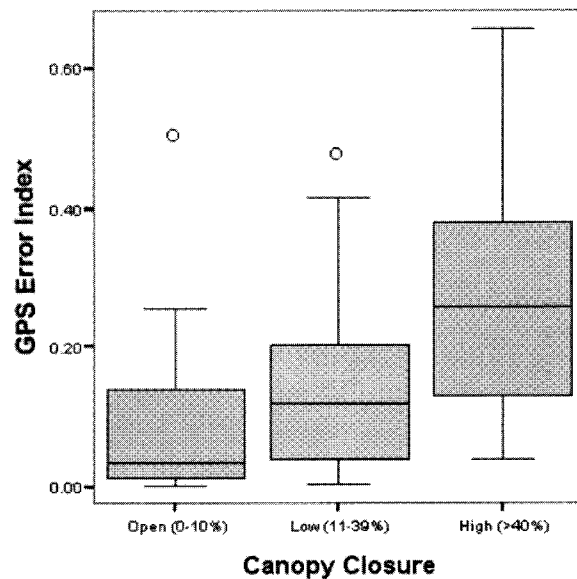


Figure 1. Box plots of GPS error index values (proportion of original GPS track length attributable to GPS error) for GPS tracks collected in each of 3 categories of canopy closure, Seeley Lake, Montana, 2004. Tukey multiple-comparison tests revealed strong differences between open and high ($\bar{y}_{\text{high}} - \bar{y}_{\text{open}} = 0.190$, $P < 0.001$) and low and high ($\bar{y}_{\text{high}} - \bar{y}_{\text{low}} = 0.121$, $P = 0.008$), and no difference between open and low ($\bar{y}_{\text{low}} - \bar{y}_{\text{open}} = 0.070$, $P = 0.178$).

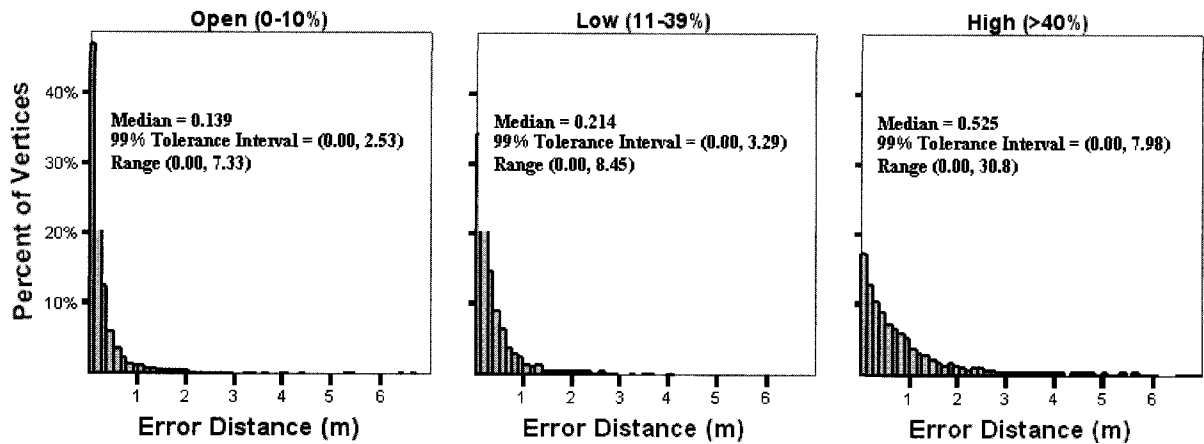


Figure 2. Histograms showing the distributions and variability of error distances associated with each vertex of GPS track data collected under three different categories of canopy closure, Seeley Lake, Montana, 2004. Tolerance intervals are distribution-free intervals containing 99% of error distances with 95% confidence.

Scale of Error

Error distances, measured from each GPS track vertex ($n=9,817$), ranged from 0–31 m, and histograms by canopy type revealed that high canopy-closure forests were associated with track vertices of larger and more variable error (Figure 2). Errors were manifested as oscillations, or “zig-zag,” about the true path, causing an increase in track tortuosity as canopy increased (Figure 3).

Median error distances were small ($M_{\text{open}}=0.139$ m, $M_{\text{low}}=0.214$ m, $M_{\text{high}}=0.532$ m) but increased with canopy. Error distance tolerance intervals indicated with 95% confidence that 99% of errors were within 0.00–2.53 m, 0.00–3.29 m, and 0.00–7.98 m for open-, low-, and high-canopy forests, respectively. Errors were greatest under high canopy, with 99% of error distances ≤ 7.98 m of the true track. This latter value sets the scale-threshold at which movements can no longer be biologically interpreted; thus, in an analysis of actual movement data, only movements that deviate ≥ 7.98 m from straight should be

treated as actual movement instead of GPS error.

Confounding sources of error

One-way ANOVA showed insignificant differences across canopy closure for user speed ($F_{2,80}=1.461$, $P=0.238$), available satellites ($F_{2,92}=0.696$, $P=0.501$), available PDOP ($F_{2,92}=0.077$, $P=0.926$), and slope ($F_{2,92}=1.44$, $P=0.241$). Thus, we expect that error caused by these sources was relatively

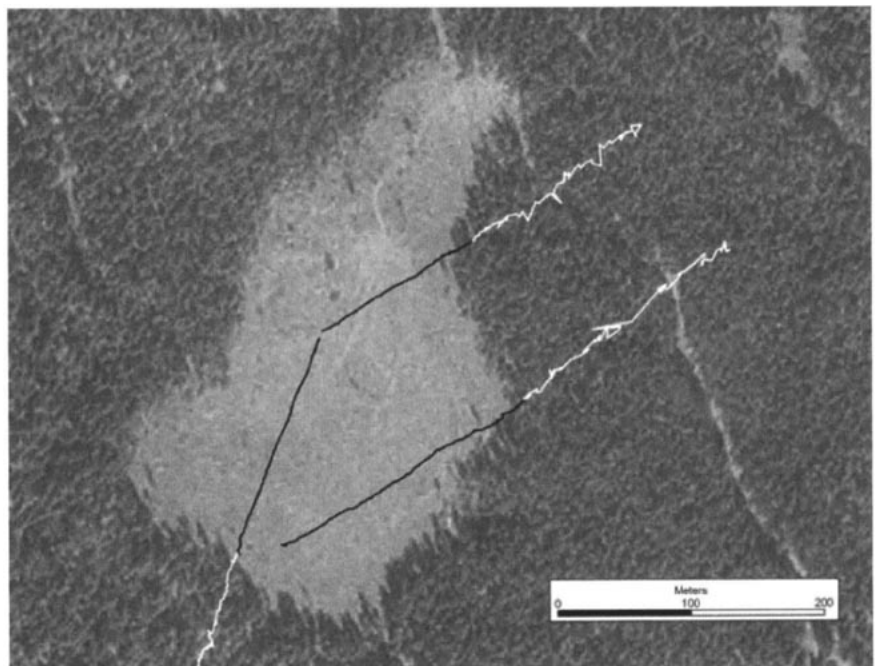


Figure 3. Straight-line test tracks ($n=6$, displayed) overlaid on a 1995 USGS digital orthophoto quadrangle reveal visual differences in GPS error between open (black line) and high (white line) canopy closure, Seeley Lake, Montana, 2004.

consistent across canopy-closure types and did not confound our analysis. As a concluding test, an ANOVA of the maximum PDOP actually achieved during tracks of each canopy type did reveal differences ($F_{2,92}=4.67, P=0.012$). While available satellite configurations were equal across canopy types, forest canopy did appear to interfere with the satellite pseudoranges actually received by the GPS units.

Discussion

Our study demonstrates that GPS error, as caused by forest canopy, has the potential to create bias in movement data. Such habitat-induced bias can lead to spurious measures of movement and type I errors in data analysis. The mean error index (\hat{e}) under high canopy was 0.275; thus, an average of 27.5% of track length recorded under high canopy was attributable to GPS error. Preliminary inspection of actual track data suggested that this percentage could be larger under the wide range of forest and topographic conditions encountered during actual snow-tracking sessions (J. R. Squires, United States Forest Service - Rocky Mountain Research Station, unpublished data).

These data were collected with Trimble GeoExplorer 3 data loggers, and the effect of canopy may differ among GPS manufacturers and units (Walton et al. 2001, Di Orio et al. 2003); we were unable to test differences among GPS units. Global Positioning System error also may vary across seasons (Dussault et al. 1999), ecotypes (Dussault et al. 1999), or topographic conditions (D'Eon et al. 2002), and we encourage caution when extrapolating our results to different study sites. Ideally, we recommend that researchers complete a similar test with project-specific methods and conditions before analyzing GPS tracking data.

We used a 2-second log interval between the collection of each GPS point along tracks. This interval affects the resolution with which tracks are recorded and may influence the scale of incurred error. With our data, this error was represented by spikes in the GPS track ≤ 31 m away from the true path. Global Positioning System tracking studies of vagile animals using deployed collars and much greater log intervals (>30 minutes) are quantifying movement at a much coarser scale and are unlikely to be affected by this fine level of error. These studies may be more troubled by differing fix rates among habitat types (D'Eon 2003, Frair et al. 2004).

However, GPS units have been deployed with very frequent log intervals (as low as 1-second, Biro et al. 2002, Weimerskirch et al. 2002), or handheld units have been used to snow-track (Ciucci et al. 2003) or follow (Pochron 2001) animals. Data collected with these frequent intervals may be affected by the canopy-associated error described in this paper. In such cases the effects of canopy should be considered before interpreting any measures of track length or tortuosity.

High- ($>40\%$) canopy forests caused greater error than low- (10–39%) and open- (0–10%) canopy forests, whereas low and open did not differ. This suggests that a nonlinear, or asymptotic, relationship may exist between canopy closure and GPS accuracy. Previous studies have generally used linear statistics to evaluate this relationship (Rempel et al. 1995, D'Eon et al. 2002) when there may in fact be some minimum threshold of canopy closure required before GPS accuracy is affected.

Global Positioning System depictions of animal movement may require some editing before further interpretation. The first step is to remove the obvious anomalies or "impossible" points often found in GPS data (D'Eon et al. 2002). Manual editing cannot, however, objectively remove the fine-scale oscillations that still obscure the true path when canopy-associated error is present (Figure 3). Smoothing algorithms, such as the Bezier algorithm in the ET GeoWizards extension for ArcGIS Desktop 8.x, offer an objective and repeatable method of removing error. Before smoothing, it is important for researchers to identify the scale at which error is affecting their GPS tracking data. The scale of this oscillating error represents the scale at which movements can no longer be biologically interpreted and should be used to set a minimum scale of movement analysis. In other words, any deviations from a straight line that occur below this minimum scale may be attributable to error rather than truth. In our case the Bezier smoothing algorithm removed the finest-scale oscillations caused by forest canopy and estimated a line that best represented the movement path through the landscape. Any smoothing procedure will result in the loss of information by reducing turning angles at each sampling interval to an artificially smooth, averaged path. However, this smoothed path is a more conservative representation of the movement path, given that deviations at the finest resolution may be fraught with bias.

To quantify the scale of GPS error, we calculated

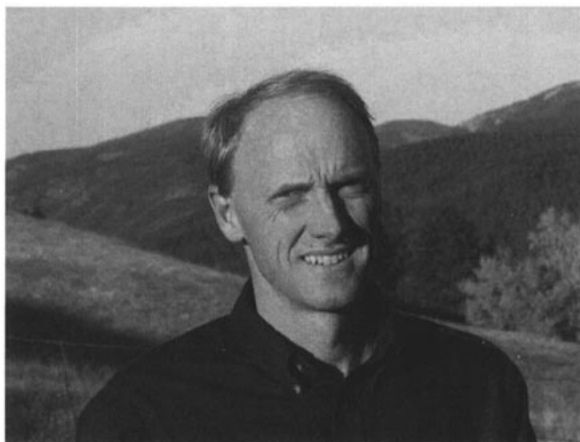
error distances for each track vertex to generate a distribution of errors among canopy types. These error distances may underestimate actual GPS error slightly because they are calculated as perpendicular distances from the true line, without accounting for the angle of error. For this reason, we used conservative 99% tolerance intervals to identify the scale of error for each canopy category, and the largest of these estimates sets our minimum scale for future movement analysis. Median error distances were <1 m for all canopy categories, and tolerance intervals suggested that most errors were ≤ 7.98 m (Figure 2). Much error was within the predicted 1-5-meter precision of GeoExplorer 3 units, but the effects of forest canopy did widen the range of expected error. Though error at this scale might seem negligible, its cumulative effect may insert a considerable bias on estimates of track length and tortuosity.

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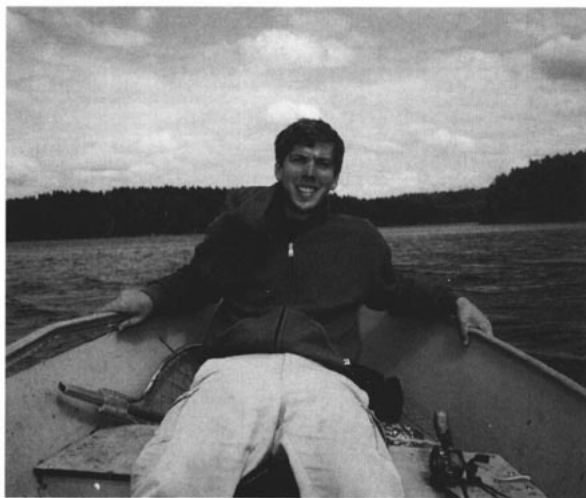
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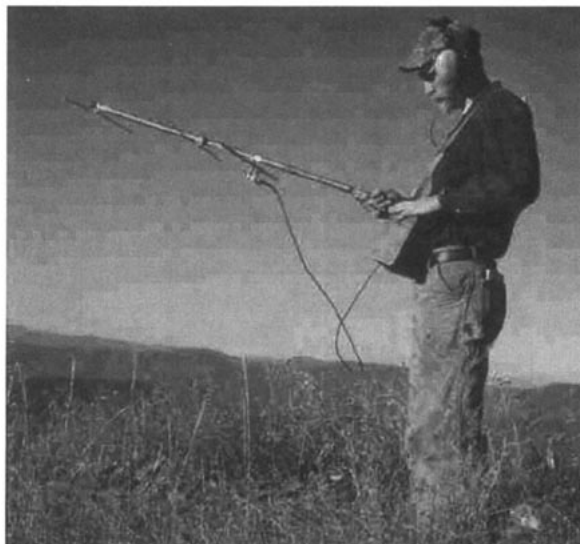
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